

THE MALE GENITALIA OF THE FAMILY ATEMNIDAE (PSEUDOSCORPIONES)

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ABSTRACT. Knowledge of the male genitalia of the Atemnidae is still limited, although several authors have previously contributed to our understanding of their structure. This study deals with the morphology and configuration of the male genital organs. Forty-four species belonging to 16 different genera have been investigated, including species of 4 genera of Miratemninae. *Anatemnus longus* Beier 1932 is synonymized with *A. voeltzkowi* (Ellingsen 1908), *Paratemnoides ceylonicus* (Beier 1932) is synonymized with *P. pallidus* (Balzan 1892), and *P. minor* (Balzan 1892) with *P. nidificator* (Balzan 1888). *Tamenus equestroides* (Ellingsen 1906) is moved to the genus *Cyclatemnus*. The genitalia of the investigated specimens are described and a general diagnostic description of the male genitalia of the family is given. The study reveals an overall uniformity in the genitalic configuration of the family, which indicates monophyly. With respect to the affinities with other families of the Cheliferoidae, the male genitalia suggest that the Atemnidae might be closer to the Withiidae than to the Cheliferidae or Chernetidae. Claimed differences between the Atemninae and Miratemninae are considered, but the morphology of the male genitalia does not support their division into two families. Comparison of species of the genera *Anatemnus*, *Catatemnus*, *Oratemnus* and *Paratemnoides* reveals greater variation within the genera than between different genera. This infers that the present systematic grouping of species does not reflect true phylogenetic relationships within the family.

Keywords: Arachnida, pseudoscorpion, genitalia, morphology, phylogenetic relationships

The male genitalia of pseudoscorpions are used for indirect sperm insertion, the male produces a spermatophore with a sperm packet on a stalk which is deposited on the substratum. The female is later inseminated from the sperm in this spermatophore. Accordingly the male has no copulatory organ, but the whole of the male genitalia is internally situated with the opening located between the second and third sternite of the abdomen. The spermatophore is produced in the chitinized genital chamber with its diverticula and associated glands. The genitalia can have a complex structure, which to a certain degree is reflected in a correspondingly complex structure of the spermatophore. The complex structure of the genitalia is perhaps most pronounced in the Cheliferoidae which includes the family Atemnidae, and may have potential in systematic work.

Several authors have dealt with the morphology of the male genitalia of species in the family Atemnidae, most extensively Vachon (1938a); but others have contributed, notably Chamberlin (1931, 1939, 1947), Dashdamirov and Schawaller (1993), Dumitresco and Orgh-

idan (1969), Heurtault (1970) and Harvey (1988).

The complex structure and the internal location makes the genitalia difficult to examine in situ, this may be part of the reason why the knowledge of the morphology is still rather limited and has been used very little for diagnostic characters in the description of genera and species. However, an early attempt to discriminate taxonomically between different species in the genera *Catatemnus* Beier 1932, *Cyclatemnus* Beier 1932 and *Tamenus* Beier 1932 was made by Vachon (1938b).

Traditionally the delimitation of the family Atemnidae and the diagnoses of the different genera in the family was thus based on external characters. The family was erected by Chamberlin (1931) and subdivided into several genera by Beier (1932a, 1932b). Beier further divided the family into two subfamilies, Atemninae and Miratemninae. The Miratemninae was elevated to full family level, Miratemnidae by Dumitresco and Orghidan (1970), partly based on their investigation on the male genitalia of *Diploatemnus insolitus* Chamberlin 1933 and its difference in orien-

tation compared to the Atemninae. But Harvey (1991, 1992) did not accept the family status of the miratemnids. He argued against it and returned them to the family Atemnidae.

The subfamily Atemninae comprises genera which have a problematic taxonomic position. The delimitations of the genera are based on external characters which on several occasions appear to be continuous and thus of less diagnostic value. This implies that the present delimitations of the genera probably do not reveal the true relationship between them. In this context, it might be valuable to make a broader survey of male genitalia both of the Miratemninae and the Atemninae, in an attempt to use these organs in the delimitation of monophyletic taxa.

METHODS

This investigation is based on the examination of male genital organs from the following 44 species representing 16 of the 19 extant genera, including species of four genera of Miratemninae. The nomenclature follows the catalogue of Harvey (1991).

Abbreviations.—AUC = Agder University College, Norway; BPBM = Bernice P. Bishop Museum, Honolulu; CAS = California Academy of Sciences, San Francisco; MHNG = Muséum d'Histoire naturelle, Geneva; NHMW = Naturhistorisches Museum, Wien; NMP = Natal Museum, Pietermaritzburg; NRMS = Naturhistoriska Riksmuséet, Stockholm; RMCA = Royal Museum of Central Africa, Tervuren; SMNS = Staatliches Museum für Naturkunde, Stuttgart; TMP = Transvaal Museum, Pretoria; WAM = Western Australian Museum, Perth; ZMB = Museum für Naturkunde, Humboldt-Universität, Berlin; ZMUO = Zoological Museum, University of Oslo.

Family Atemnidae Chamberlin 1930

Subfamily Miratemninae Beier 1932

Brazilatemnus browni Muchmore 1975

Material examined.—BRAZIL: Pará, Porto Trompetas, August 1992, J.D. Majer leg. (WAM; Harvey det.).

Diplolemnus insolitus Chamberlin 1933

Material examined.—SPAIN: Gran Canaria, Maspalomas, dunes, 16 March 1994, C. Wurst leg. (SMNS, no. 3448; Schawaller det.).

Miratemnus hirsutus Beier 1955

Material examined.—SOUTH AFRICA: Pretoria, 1958 (RMCA; Beier det.); Cape Province, Cape Houtbaai, December 1960 (TMP, no. ZA 46; Klausen det.); E. Cape, Grahamstown, Harpers Hall, October 1943, W. G. Rump leg. (NMP, no. 668). RHODESIA (ZIMBABWE): Inyanda, February 1969, R. Mussard leg. (MHNG; Beier det.).

Miratemnus kenyaensis Mahnert 1983

Material examined.—KENYA: Namanga, 21 March 69, Å. Holm leg. (MHNG; paratype); Lake Elmenteita, 1800 m, SS. pierres (under stones?), 7 November 1977, Mahnert & Perret leg. (MHNG; paratype).

Miratemnus zuluanus Lawrence 1937

Material examined.—SOUTH AFRICA: KZN, Drummond, February 1942, W.G. Rump leg. (NMP, no. 661; Beier det.).

Tullgrenius indicus Chamberlin 1933

Material examined.—INDIA: Tamil Nadu; Amman Nagar, N. of Coimbatore, 6 December 2000, F. Klausen leg. (AUC; Klausen det.).

Subfamily Atemninae Chamberlin 1930

Anatemnus angustus (Redikorzev 1938)

Material examined.—VIETNAM: Plateau Lang Biang (= Cao Nguyên Lâm Viên), 1938–39, C. Dawydoff leg. (NHMW; Beier det.).

As *Oratemnus indicus*: INDIA: Mysore, 12 mil. E of Virajpet, 24 February 1962, Ross & Cavagnaro leg. (CAS; Beier det.).

As *Anatemnus nilgiricus*: INDIA: Mysore, 8 mi. NE Mercara, 1000 m, 22 February 1962, E. S. Ross & D. Q. Cavagnaro leg. (CAS; Beier det.).

Remarks.—The specimens identified as *O. indicus* and *A. nilgiricus* are, as far as I can judge, both in configuration of the genitalia and in outer morphology identical to *A. angustus*. The specimens of *O. indicus* have been compared with the holotype of *Chelifer indicus* deposited in Zoological Museum in Copenhagen and the description given by With (1906). The dorsal tubercle of the trochanter of the holotype is blunt ended and not pointed as in the specimens in my custody. I have not been able to compare the specimen identified as *A. nilgiricus* with the type ma-

terial in the Roewer collection. However, in the description given by Beier (1932a) of *A. nilgircicus*, he states that the dorsal tubercle of the trochanter is blunt ended or rounded, contrary to the specimen above which has a conical and pointed dorsal tubercle.

The genitalia of *A. angustus* are identical with those of the syntype of *Catatemnus birmanicus* from Naturhistoriska Riksmuséet, Stockholm. Moreover, apart from the appearance of the carapace of *C. birmanicus* they are similar in external morphology. That is, the shape of the trochanter and patella of the pedipalps are similar, the trichobothria of the fingers have the same configuration and so have the tergal seta of the abdomen.

Anatemnus elongatus (Ellingsen 1902)

Material examined.—ECUADOR: As *Chelififer (Atemnus) elongatus*: by Guayaquil, June 1901, Ortoneda leg. (ZMUO, no.102; syntype)

Anatemnus javanus (Thorell 1883)

Material examined.—PAPUA NEW GUINEA: As *Chelififer (Atemnus) javanus*: Bismarck Archipelago, Fr. Dahl leg. (ZMUO, no. 319; Ellingsen det.).

Anatemnus novaguineensis (With 1908)

Material examined.—PAPUA NEW GUINEA: Finschhafen, 17 April 1944, E. S. Ross leg. (CAS; Beier det.).

Anatemnus orites (Thorell 1889)

Material examined.—As *Chelififer* (= *Anatemnus*) *orites*: BURMA (MYANMAR): Thenasserim, Plapoo, Fea leg. (NRMS, no. 6; Coll.[ection of?] Thorell); [Probably Carin Ghecu, Tao, 13–1400 m, 1885–1887], Fea leg. (ZMUO, no. 566; Ellingsen det.).

As *Chelififer* (= *Oratemnus*) *indicus*: INDIA: Gravely, 1912 (ZMUO, no. 593; Ellingsen [?] det.).

Remarks.—The specimens identified as *A. orites* have been compared with syntypes of *Chelififer orites* from Zoological Museum in Copenhagen. They are identical in outer morphology, and so is the specimen identified as *Chelififer indicus* which has been compared with the holotype of *C. indicus*. The only divergence is the form of the conical dorsal tubercle of the trochanter which is slightly higher in the holotype of *C. indicus*.

The genitalia of *A. orites* are very similar to those of *A. angustus*. With respect to the characters of the outer morphology they are similar except for the conical dorsal tubercle of the trochanter which is blunt ended in *A. orites* and pointed in *A. angustus*.

Anatemnus subvermiformis

Redikorzev 1938

Material examined.—VIETNAM: Plateau Lang Biang [= Cao Nguyên Lâm Viên], 1938–39, C. Dawydoff leg. (NHMW; Beier det.).

Anatemnus voeltzkowi (Ellingsen 1908)

Chelififer (Atemnus) voeltzkowi elongata Ellingsen 1908: 488 (junior primary homonym of *Chelififer (Atemnus) elongatus* Ellingsen, 1902).

Anatemnus longus Beier 1932: 586 (replacement name for *Chelififer (Atemnus) voeltzkowi elongata* Ellingsen 1908). NEW SYNONYMY.

Material examined.—As *Chelififer (Atemnus) voeltzkowi*: MADAGASCAR: SW Madagascar, Voeltzkow leg. (ZMUO, no. 307; syntype).

As *Chelififer (Atemnus) voeltzkowi elongata*: MADAGASCAR: Marovoay, September 1906, W. Kaudern leg. (ZMUO, no. 336; syntype).

Remarks.—The specimens of *A. voeltzkowi* and *A. longus* in ZMUO are unquestionably syntypes, the rest of the type series being deposited in the Zoological Museums in Berlin and in Stockholm. *Anatemnus longus* was originally described by Ellingsen (1908) as a variety of *A. voeltzkowi*. I can find no significant differences in external morphology between the two and the male genitalia are identical. Accordingly I consider *A. longus* as a synonym of *A. voeltzkowi*.

Atemnus politus (Simon 1878)

Material examined.—ITALY: prov. Basilicata, Lido San Basilia, comm. Metaponta, sieving in *Pinetum* near shore, 4 September 1993, V. Mahnert leg. (MHNG; Mahnert det.). SPAIN: Rincon de Ademuz, N. Puebla de San Miguel, *Quercus* forest, 22 April 1984, Schawaller leg. (SMNS, no 1057; Schawaller det.); Mallorca, Road between Poreres and Vilafranca, 5 May 2000, under stones in *Quercus ilex* forest, F. Klausen leg. (AUC; Klausen det.). TURKEY: Anatolien, Akzehir, 22 April 1960 (NHMW; Beier det.).

Atemnus syriacus (Beier 1955)

Material examined.—TURKEY: Köyceğiz, 17 February 1969 (NHMW; Beier det.).

Athleticatemnus pugil Beier 1979

Material examined.—As *Cyclatemnus granulatus*: BELGIAN CONGO (DEMOCRATIC REPUBLIC OF CONGO): Kivu, Terre Kalehe, Frangi, 18 August 1960, Musanola & Kangeta leg. (RMCA, no. 118.580; Beier det.).

Remarks.—Although Beier (1979) placed this genus close to *Titanatemnus* in his description of the species, the single specimen identified by me is very similar to *Cyclatemnus granulatus* in external morphology. Apart from the shallow or very blunt dorsal tubercle of the trochanter in *A. pugil* (which is pointed in *C. granulatus*) the characters are similar including the configuration of discal setae on the tergites. Admittedly, the palpal hand of *A. pugil* is very robust in the dorsoventral direction, but so is the palpal hand of *C. granulatus*, even if this is slightly less so. The male genitalia is closer to *Cyclatemnus* in appearance than to *Titanatemnus*, although it is not similar to *C. granulatus*.

Catatemnus birmanicus (Thorell 1889)

Material examined.—BURMA (MYANMAR): Bhamô (NRMS; syntype, Doria ded. [sic]).

As *Chelifer (Anatemnus) orites*: INDONESIA: Sumatra, [probably: Si-Rambé or Pangherang-Pisang, 1891/94, E. Modigliani leg.] (ZMUO, no. 539, Ellingsen det.).

Remarks.—The syntypes from Naturhistoriska Riksmuséet, Stockholm have been compared with the syntypes from Zoological Museum in Copenhagen. They are all identical in outer morphology and thus seem to be a homogenous group of syntypes.

The species (and genus) are separated from those of *Anatemnus* and *Oratemnus* by the character of the carapace, given as a transversal furrow or "Querfurche" by Beier (1932a, 1932b). As remarked under the species *A. angustus* and *A. orites*, the genitalia of these two are similar or identical to *C. birmanicus*, which seem to contradict the separation of them in different genera.

Catatemnus granulatus Mahnert 1978

Material examined.—CAMEROON: S.Kribi, Rocheur de Loup 17 February 1980, primary forest, Ferrara & Schlogal leg. (SMNS, no. 513; Mahnert det.).

As *Cyclatemnus burgeoni*: BELGIAN CONGO (DEMOCRATIC REPUBLIC OF CONGO): Ibembo, February 1952, R.F. Hutsebaut leg. (RMCA, no. 72.809; Beier det.).

Catatemnus togoensis (Ellingsen 1910)

Material examined.—NIGERIA: Lagos, Iseri, 26 March 1949 [1929?], Malkin leg. (NHMW; Beier det.). GHANA: Akumadan 2 September 1966. 350 m. E.S. Ross & K. Lortzen leg. (CAS; Beier det.).

As *Catatemnus congicus*: BELGIAN CONGO (DEMOCRATIC REPUBLIC OF CONGO): 50 km. S. of Chela, 26 July 1957. Ross & Leech leg. (CAS; Beier det.).

As *Cyclatemnus fallax*: KENYA: Kaiomosi Mission, 27 mi. NE of Kisumu, 1650 m, 29 November 1957 (CAS; Beier det.).

As *Tamenus femoratus* (in part): IVORY COAST: Divo, 16 August 1963. J. Decelle leg. (RMCA, no. 161.132; Heurtault det.).

As *Chelifer (= Titanatemnus) sjoestedti*: CAMEROON: (no locality and date given), Y. Sjöstedt leg. (NRMS; Tullgren det.); Itoki, February 1891, Y. Sjöstedt leg. (NRMS; included in syntype material of *Chelifer sjoestedti*, Tullgren det.).

Remarks.—The identification of *C. togoensis* as *T. sjoestedti* is probably due to a misinterpretation of the specimens as juveniles of *T. sjoestedti*. The 4 males and 3 females from the vial with no locality and date given were labeled juveniles. The same explanation probably applies for the single specimen included in the type material of *T. sjoestedti* (12 males, 15 females, 1 juvenile). Both outer morphology and genitalia tell that these specimens are undoubtedly *C. togoensis*.

Cyclatemnus burgeoni (Beier 1932)

Material examined.—BELGIAN CONGO (DEMOCRATIC REPUBLIC OF CONGO): Kuri, terr. de Kabare, Bitale, 1600 m, 29 June 1951, N. Leleup leg. (RMCA, no. 110949–110950; Beier det.).

Cyclatemnus centralis Beier 1932

Material examined.—BELGIAN CONGO (DEMOCRATIC REPUBLIC OF CONGO):

Katanga, Terr. d'Alberville, mont. Kabobo, Ht. Kiyambi, 1700 m, September 1958, N. Leleup leg. (RMCA, no.112.741; Beier det.). RUANDA (RWANDA): 78 km W. of Astrida, 1957 (CAS; Beier det.).

Cyclatennus dolosus Beier 1964

Material examined.—RHODESIA (ZIMBABWE): Northern Rhodesia, Abercorn, gallery forest, Riwer Mwengo, 8 miles N. of Abercorn, 1800 m, June 1960, N. Leleup leg. (RMCA, no.15.078; Beier [?] det.).

Cyclatennus equestroides

(Ellingsen 1906), NEW COMBINATION

Material examined.—EQUATORIAL GUINEA: Isl. Fernando Póo [Bioko], Punta Frailes, October 1901, L. Fea leg. (ZMUO, no. 217; syntype). PORTUGUESE GUINEA (GUINEA-BISSAU): Rio Cassine, February–April 1900, L. Fea leg. (ZMUO, no. 218; syntype).

Remarks.—Although these specimens are not labelled as type material, the collection details leave no doubt they form part of the type material used by Ellingsen (1906) in his description of the species. The remainder of the type material is deposited in the Museo Civico di Storia Naturale, Genova.

Beier (1932a, 1932b) placed this species in the genus *Tamenus*, but was clearly in doubt about this decision. After examining the specimens, it is quite clear that they do not belong in *Tamenus*. They lack a transverse groove on the carapace as Ellingsen (1906) himself pointed out, and the configuration of the trichobothria is different. On the other hand, these characters fit very well with those of *Cyclatennus*. The difference between *C. equestroides* and the *Cyclatennus* spp. investigated by me is that the palpal patella of *C. equestroides* is slightly broader seen in lateral view. The male genitalia are almost identical to those of *Cyclatennus centralis*. Accordingly I transfer this species to the genus *Cyclatennus*.

Cyclatennus globosus Beier 1947

Material examined.—SOUTH AFRICA: E. Cape, Pirie Forest, March 1937, R.F. Lawrence leg. (NMP; Beier det.).

Cyclatennus granulatus Beier 1932

Material examined.—IVORY COAST: Bingerville. 16 April 1962, J. Decelle leg.

(RMCA, no. 121.999; Beier det.). CAMEROON: 10 mi. W. Bertona, 640 m, 5 October 1966, Ross & Lorentzen leg. (CAS; Beier det.).

Cyclatennus minor Beier 1944

Material examined.—KENYA: Athi River, 1500 m, 19 October 1957, Ross & Leech leg. (CAS; Beier det.).

Cyclatennus robustus Beier 1959

Material examined.—BELGIAN CONGO (DEMOCRATIC REPUBLIC OF CONGO): Tshibinda, February 1932 (RMCA, no. 54.233–54.234; Beier det.); Nioka, October 1953 (RMCA, no. 80.090; Beier det.). TANZANIA: TANGANYIKA?: 12.miles NE of Sumbawanga (RMCA, no. 116.008; Beier det.);

Micratennus crassipes Mahnert 1983

Material examined.—KENYA: Nakuru, Lake Elmenteita, SS. pierres [under stones?], 1900 m, 7 November 1974, Mahnert & Perret leg. (MHNG; paratype).

Oratennus loyolai Sivaraman 1980

Material examined.—INDIA: Tamil Nadu, Redhills, Madras, 6 August 1976 (MHNG; paratype); Tamil Nadu, Ganesaduram, N.of Coimbatore, 6 December 2000, K.R. Klausen & F. Klausen leg. (AUC; F. Klausen det.); Karnataka, Mysore, park by Ghandi Square, 29 November 2000, K.R. Klausen & F. Klausen leg. (AUC; F. Klausen det.). SRI LANKA: Peradeniya, Kandy District, Botanical Garden, 20 February 2000, D. Huber leg. (AUC; F. Klausen det.).

Oratennus navigator (With 1906)

Material examined.—INDONESIA: Java, Batavia, March 1889, L. Loria leg. (ZMUO, no. 377; Ellingsen [?] det.); Bali, Brama Kutri, Singapadu, 12 March 1999, K.R. Klausen & F. Klausen leg. (AUC; F. Klausen det.); Between Papuan and Bantran, 10 March 1999, K.R. Klausen & F. Klausen leg. (AUC; F. Klausen det.). MALAYSIA: East Coast, 17 km N of Kuantan, 31 March 2002, F. Klausen leg. (AUC; F. Klausen det.).

As *Oratennus brevidigitatus*: SEYCHELLES: Praslin, Cote d'Or, 30 July 1982, C.I. Voucher leg. (MHNG; Mahnert det.).

As *Oratennus philippinensis*: PHILIP-

PINES: Luzon isl., Kiangan/Ifugao, 1982, Margraf leg. (SMNS, no. 1543; Schawaller det.).

As *Oratemnus saigonensis*: THAILAND: Doi Sutep, E slope, 260 m, 15 July 1962, E. S. Ross & D.Q. Cavagnaro leg. (CAS; Beier det.).

Remarks.—The material from the Zoological Museum in Oslo and the material collected by me on Bali and in Malaysia has been compared with the description given by With (1906) of *Oratemnus navigator* and the holotype from Zoological Museum in Copenhagen. There is no doubt that they are identical. Moreover, when Schawaller (1994) synonymized *O. saigonensis* with *O. semidivisus*, he suggested that *O. navigator* belongs to the same species together with *O. proximus*, *O. loyolai* and *O. yodai*. *Oratemnus loyolai* is definitely not conspecific with the others, judging from its very different and characteristic genitalia. However, the male genitalia of the others investigated by me are identical. Since the investigated specimens listed above of *O. brevidigitatus*, *O. philippinensis* and *O. saigonensis* (= *O. semidivisus*) have been identified by very able specialists, there is a possible synonymy, perhaps together with *O. proximus* and *O. yodai*.

Oratemnus punctatus (L. Koch 1885)

Material examined.—AUSTRALIA: Queensland, 55 km N. of Goomeri, 23 January 1982, M. Baehr leg. (SMNS, no.898; Harvey det.).

Paratemnoides ellingseni (Beier 1932)

Material examined.—MOZAMBIQUE: Chitengo, Gorongosa Game Reserve, September 1957, R.F. Lawrence leg. (NMP, no. 5155; Beier det.). MADAGASCAR: Morondava, Betela Mission Station, 20 February 1998, Klausen leg. (AUC; Klausen det.). SOUTH AFRICA: Zululand, 1938 (NHMW; Beier det.); KZN, Gollel, August 1938, R.F. Lawrence leg. (NMP, no. 630; Beier det.); Lovedale, on trees (TMP, no. 4899; Judson det.). UGANDA: Apac District, Aboke, near St Marys College, 16 May 2002, Klausen leg. (AUC; Klausen det.); Kampala, Golf Course, 18 May 2002, Klausen leg. (AUC; Klausen det.).

As *Paratemnus pallidus* (in part): BELGIAN CONGO (DEMOCRATIC REPUBLIC

OF CONGO): Garamba, 1951 (NHMW; Beier [?] det.).

As *Paratemnus braunsi*: ETHIOPIA: Bahar Dar, 12 October 1968, K.W. and H. Harde leg. (SMNS, no. 202; Beier and Mahnert det.).

Remarks.—The identification as *P. braunsi* raises the question of a possible synonymy. The species was placed in *Catatemnus* by Beier (1932a), obviously due to what he interpreted as a transverse furrow on the carapace. However, when Tullgren (1907) described the species based on one female, he explicitly wrote that “Querfurchen fehlen vollständig, nur auf der Mitte da, wo die zweite Furche sein sollte, bemerkt man einen kleinen Eindruck.” In a paper by Weygoldt (1970), some of the material used and identified by Beier is referred to as *Paratemnus braunsi*, which suggests that Beier was aware of a misplacement in *Catatemnus*. So indicates this identification by Beier and Mahnert. The specimen investigated by me is decidedly a *P. ellingseni*, but since I have not investigated the type of *C. braunsi* deposited in the Natural History Museum in Hamburg, I leave it as a misidentification for the moment.

Paratemnoides insubidus (Tullgren 1907)

Material examined.—NAMIBIA: Kobos, 40 miles S of Rehoboth, 19 July 1937 (TMP, no. 7894; Beier det.).

Paratemnoides nidificator (Balzan 1888)

Chelifer nidificator Balzan, 1888a: no pagination, figs.

Chelifer (Atemnus) nidificator minor Balzan, 1892: 510–511, fig. 1. NEW SYNONYMY.

Material examined.—As *Paratemnus minor*: BRAZIL: Manaôs, 27 August 1973, R. Schuster leg. (MHNG, no. BR-331; Mahnert det.).

As *Paratemnoides nidificator*: BRAZIL: Mato Grosso State, Nova Mutum, Fazenda Burity, 12 June 2003, H.F. Mendes leg. (AUC; Klausen det.); Sao Paulo, Riberto Preto, 4 June 2003, H.F. Mendes leg. (AUC; Klausen det.). COSTA RICA: near Ajugas, 5 December 1996, Klausen leg. (AUC; Klausen det.); Manuel Antonio, 8 December 1996, Klausen leg. (AUC; Klausen det.); Golfito, 9 December 1996, Klausen leg. (AUC; Klausen det.).

Remarks.—Balzan (1892) described *P. minor* as a variety of *P. nidificator*. He stated that *P. minor* is insignificantly smaller than *P.*

nidificator, but the palps and the chelal hand do not differ. Contrary to this he gave the body length of *P. minor* to be 4 mm (Balzan 1892) and that of *P. nidificator* to be 3 mm (Balzan 1890). With (1908) in his description of *P. nidificator* obviously considered *P. minor* as a variety of the former. Beier (1932a, 1932b) eventually raised *P. minor* to species level, stating that the two are very similar, although *P. minor* is smaller. The dimensions given of the palps and the fourth pair of legs are slightly smaller for *P. minor*, the ratio between lengths and widths are very close to *P. nidificator*.

I have examined 55 specimens, comprising five specimens of *Paratemnoides minor* from Manaô's, Brazil as given above, two specimens as *Chelififer nidificator* from Haiti (Tullgren det.), 16 from Sao Paulo, Brazil, 16 from Mato Grosso, Fazenda Buriti, Brazil and 16 specimens from the three localities in Costa Rica as given above. Admittedly, the specimens of *P. minor* and those from Costa Rica are slightly smaller compared to the average measures of those from the other localities identified as *P. nidificator*. However, the populations of *P. nidificator* from Mato Grosso and Sao Paulo both have specimens as small as those of *P. minor*. In other words the specimens of *P. minor* are within the range of *P. nidificator*. Moreover, when comparing the ratios between the lengths and widths of the individual segments of the pedipalps and the fourth legs, they are almost identical, no matter if they are taken from *P. minor* or *P. nidificator*. The outer morphological characters are identical, so are the genital characters of the males investigated. Thus there is no diagnostic character which separates them as two species. Accordingly I consider *P. minor* as a junior synonym of *P. nidificator*.

Paratemnoides pallidus (Balzan 1892)

Chelififer (Atemnus) pallidus Balzan, 1892: 511–512, figs. 2, 2a.

Chelififer (Atemnus) guineensis Ellingsen, 1906: 246. Synonymized by Harvey (1991).

Paratemnus congicus Beier, 1932b: 566–567, fig. 7. Synonymized by Beier (1972).

Paratemnus ceylonicus Beier, 1932b: 569, fig. 8. NEW SYNONYMY.

Material examined.—As *P. ceylonicus*: S-CEYLON (SRI LANKA): Habaraduwa, 20

January–4 February 1983, T. Osten leg. (SMNS, no. 1542; Schawaller det.).

As *P. congicus*: BELGIAN CONGO (DEMOCRATIC REPUBLIC OF CONGO): Brazzaville, 11 January 1964, Balogh & Zicsi leg. (MHNG, no. 653; Mahnert det.).

As *P. guineensis*: BELGIAN CONGO (DEMOCRATIC REPUBLIC OF CONGO): Brazzaville, 27 December 1963, Balogh & Zicsi leg. (MHNG, no. 589; Mahnert det.).

As *P. pallidus*: BELGIAN CONGO (DEMOCRATIC REPUBLIC OF CONGO): Garamba, 1951, (NHMW; Beier det.). UGANDA: Kampala, Golf Course, 18 May 2002, Klausen leg. (AUC; Klausen det.). SRI LANKA: Peradeniya, Botanical Gardens, Kandy District, 20 February 2000, D. Huber leg. (AUC; Klausen det.). MALAYSIA: Kuala Lumpur, 3 April 2002, Klausen (AUC; Klausen det.).

Remarks.—The descriptions given by Beier (1932a, 1932b) for *P. pallidus* and *P. ceylonicus* indicate that the main distinction is based on differences in the dimensions and proportions of the appendages. I have compared *P. ceylonicus* (13 specimens) from Sri Lanka and Malaysia with *P. congicus* and *P. guineensis* (2 specimens) from Belgian Congo and *P. pallidus* (8 specimens) from Uganda. I can find no significant differences in the pedipalps and the 4th legs of the two groups, either in dimensions or in proportions. Moreover, in his key to the genus *Paratemnus*, Beier (1932a, 1932b) used the length of the palpal finger compared to the width of the chela as a diagnostic character to separate *P. ceylonicus* (and *P. congicus*) from *P. pallidus*. In my material all the specimens have the fixed finger longer than the width of the palpal chela. In a later publication Beier (1972) synonymized *P. congicus* with *P. pallidus* which suggests that he no longer considered this to be a discriminating character. Based on my measurements and the fact that the male genitalia are identical, I consider *P. ceylonicus* to be a synonym of *P. pallidus*.

Paratemnoides salomonis (Beier 1935)

Material examined.—SOLOMON ISLANDS: Guadalcanal, 9 May 1965 (NHMW; Beier[?] det.). PAPUA NEW GUINEA: New Britain, Volo volo, 6 July 1995, K.R. Klausen & F. Klausen leg. (AUC; F. Klausen det.); Wevak, by Windjammer Hotel, 9 July 1995, K.R.

Klausen & F. Klausen leg. (AUC; F. Klausen det.).

Stenatemnus fuchsi (Tullgren 1907)

Material examined.—INDONESIA: Nias Island, Eastcoast, Lawalo, phoretic on Passalidae, 23 September 1979, D. Erber leg. (SMNS, no. 296; Schawaller det.); Sumatra [probably: Si-Rambé, 1891–94, E. Modigliani leg.] (ZMUO, no. 538; Ellingsen det.).

Tamenus femoratus Beier 1932

Material examined.—IVORY COAST: Divo, 16 August 1963, J. Decelle leg. (RMCA, no. 83.161.132; Heurtault det.).

Titanatemnus gigas Beier 1932

Material examined.—CAMEROON: Bosum, scrub, 20 May 1914, Tessmann leg. (ZMB, no. 31190; paratype)

Titanatemnus natalensis Beier 1932

Material examined.—SOUTH AFRICA: Durban, March 1916, C. Akerman leg. (NMP, no. 5106; Beier det.).

As *Chelifer* (= *Titanatemnus*) *equester*: Natal, Durban, C.N. Barker leg. (ZMUO, no. 553; Ellingsen det.).

Remarks.—The main difference between *T. natalensis* and *T. equester* is the size, with the latter being the larger of the two. Because size is not the best of criteria for separating species, an investigation of the genitalia of *T. equester* might give a clue to their relationship.

Titanatemnus palmquisti (Tullgren 1907)

Material examined.—Kenya: Meru, 25 April 1957 (NHMW; Leleup det.). NYASSA (MALAWI?): 1899, Fülleborn leg. (ZMUO, no. 306; identified by Ellingsen det.).

Titanatemnus sjoestedti (Tullgren 1901)

Material examined.—As *Chelifer sjoestedti*: CAMEROON: Itoki, February 1891, Y. Sjöstedt leg. (NRMS: syntype). FRENCH CONGO (CONGO): N'kogo, December 1902, L. Fea leg. (ZMUO, no. 211; Ellingsen det.).

Titanatemnus tessmanni Beier 1932

Material examined.—As *Chelifer sjoestedti*: PORTUGUESE GUINEA (GUINEA-BISSAU): Rio Cassine, January–April 1900, L. Fea leg. (ZMUO, no. 210; Ellingsen det.).

Titanatemnus thomeensis (Ellingsen 1906)

Material examined.—SAO THOMÉ: Agua Izé, 400–700 m, December 1900, L. Fea leg. (ZMUO, no. 219; syntype).

The genital organs were dissected with honed steel needles under a stereomicroscope. Following 24 hours soaking in a solution of 2% pepsin in water acidified with HCl at room temperature, the organs were washed and placed in successive alcohol baths ending with a mixture of 96% alcohol and Euparal essence. I prefer this method to soaking in potassium hydroxide because it is probably more gentle to the delicate chitinized parts. The specimens were finally mounted on slides in Euparal.

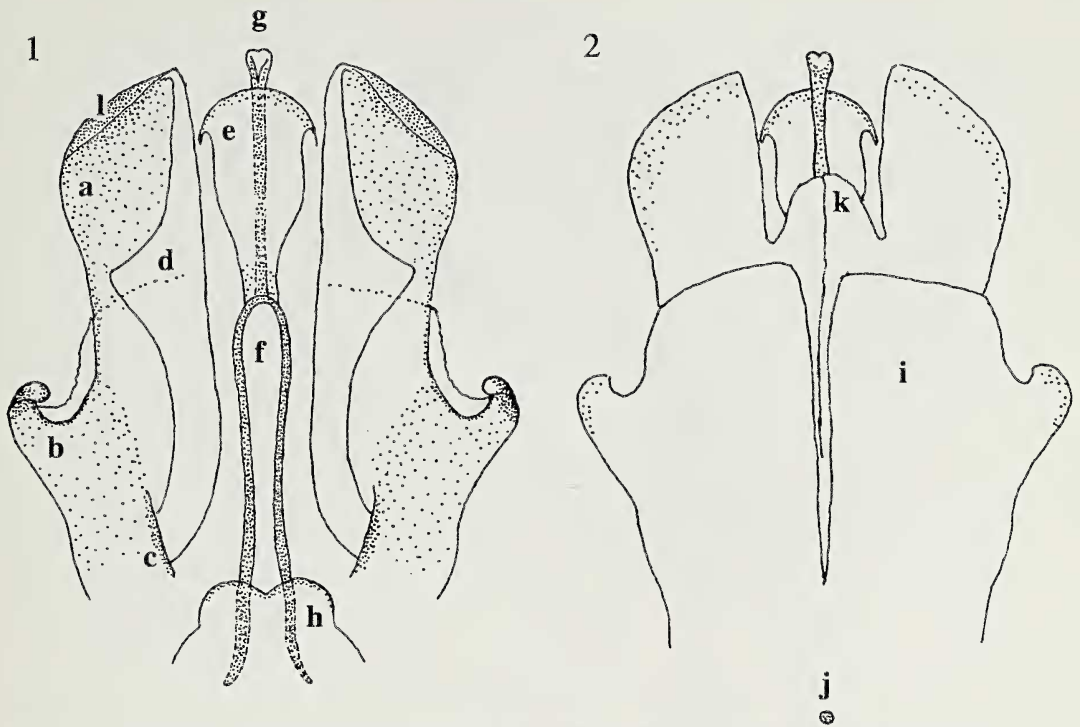
Specimens were examined and photographed under a stereomicroscope using dark-field/lightfield equipment. Drawings were made using a compound microscope with a drawing tube.

Dissection of the genital organs from the body was necessary because their orientation *in situ* makes it almost impossible to obtain a correct interpretation. Moreover, the translucent parts are particularly difficult to see in this position. All genital organs have accordingly been examined after dissection. They were orientated on the slide in a position with the lateral apodemes and lateral rods lying uppermost, horizontal to the light axis of the microscope.

DESCRIPTION OF THE GENITALIA

The description concentrates on the chitinized parts of the genitalia, i.e. the different diverticula of the genital atrium and their associated apodemes, as well as the ejaculatory canal and its atrium. Legg (1974) has given a generalized description of the genital organs of male pseudoscorpions. I have followed his terminology when possible.

The genital organ as a whole can be directed more or less anteriorly from the genital opening in some species and posteriorly in others. It is therefore confusing to use the terms dorsal and ventral side when referring to the different parts of the organ. To avoid confusion I use the term "anterior side" as the side of the organ which is connected to the anterior part of the genital aperture and "posterior side" for the side connected to posterior part of it (Figs. 3 & 4).



Figures 1-2.—Generalized view of atemnid male genitalia. Anterior side: a. lateral apodeme; b. hooked branch; c. sclerotized bar; d. longitudinal fold of medial diverticulum; e. ejaculatory canal atrium; f. lateral rods; g. dorsal apodeme; h. ventral diverticulum; l. lateral lip of lateral apodeme. Posterior side: i. dorsal diverticulum; j. apophysis of posterior dorsal gland; k. extension of medial diverticula.

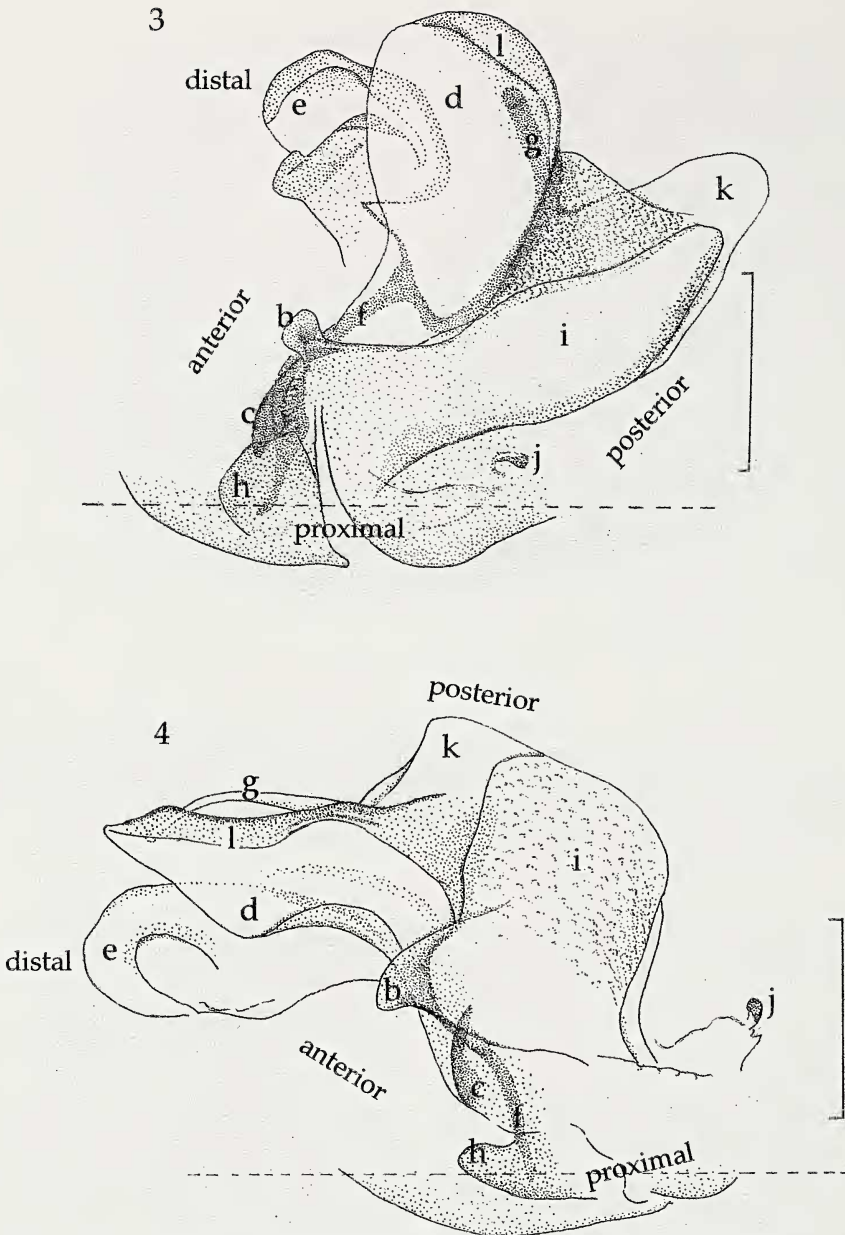
Moreover, I use the term “proximal” for the parts lying near the genital aperture and the term “distal” for parts near the seminal vesicles (Figs. 3 & 4). However, when the words are part of established terms, like in “dorsal diverticulum” or “dorsal apodeme”, I have kept them to make my descriptions compatible with that of Legg (1974).

The size of the genital organ is correlated with the size of the species: the larger species like *Titanatemnus* (Figs. 11-14) have the most prominent organs with distinctly colored apodemes; in the smaller species of *Paratemnoides* (Figs. 18-20), *Brazilatemnus* and *Stenatemnus* (Figs. 6 & 10) the organ is small, transparent and almost colorless. The specimen of *Anatemnus javanus* (Fig. 24) studied is completely colorless, but this is probably due to conservational conditions.

The most conspicuous parts on the anterior side of the organ are the lateral apodemes and the lateral rods, connected to the dorsal apodeme and the ejaculatory canal atrium (Fig. 1). The posterior side is dominated by the prom-

inent and translucent bilobed *dorsal and medial diverticula* lying side by side along the sagittal plane (Fig. 2).

Dorsal diverticula (Figs. 2, 3 & 4: i).—On the posterior side of the genital organ the proximal part of the dorsal diverticula is connected to the atrium of the posterior dorsal gland with its support and rugose entrance area. The posterior dorsal gland is attached to this area which has a small, knob-shaped apophysis (Figs. 2, 3 & 4: j). Distally the dorsal diverticula are confined by a transverse fold overlying the medial diverticula and running between the hooked branches of the two lateral apodemes (Figs. 1, 3 & 4: b). On the lateral side of the dorsal diverticula the surface is very rugose. It is made up of a dense layer of more or less conical tubercles, each with a minute hole in the utmost tip. They obviously are the seat of glands, like the entrance area of the posterior dorsal gland. In most species the dorsal diverticula are almost fused in the sagittal plane on the posterior side. The dorsal diverticula are extended lat-

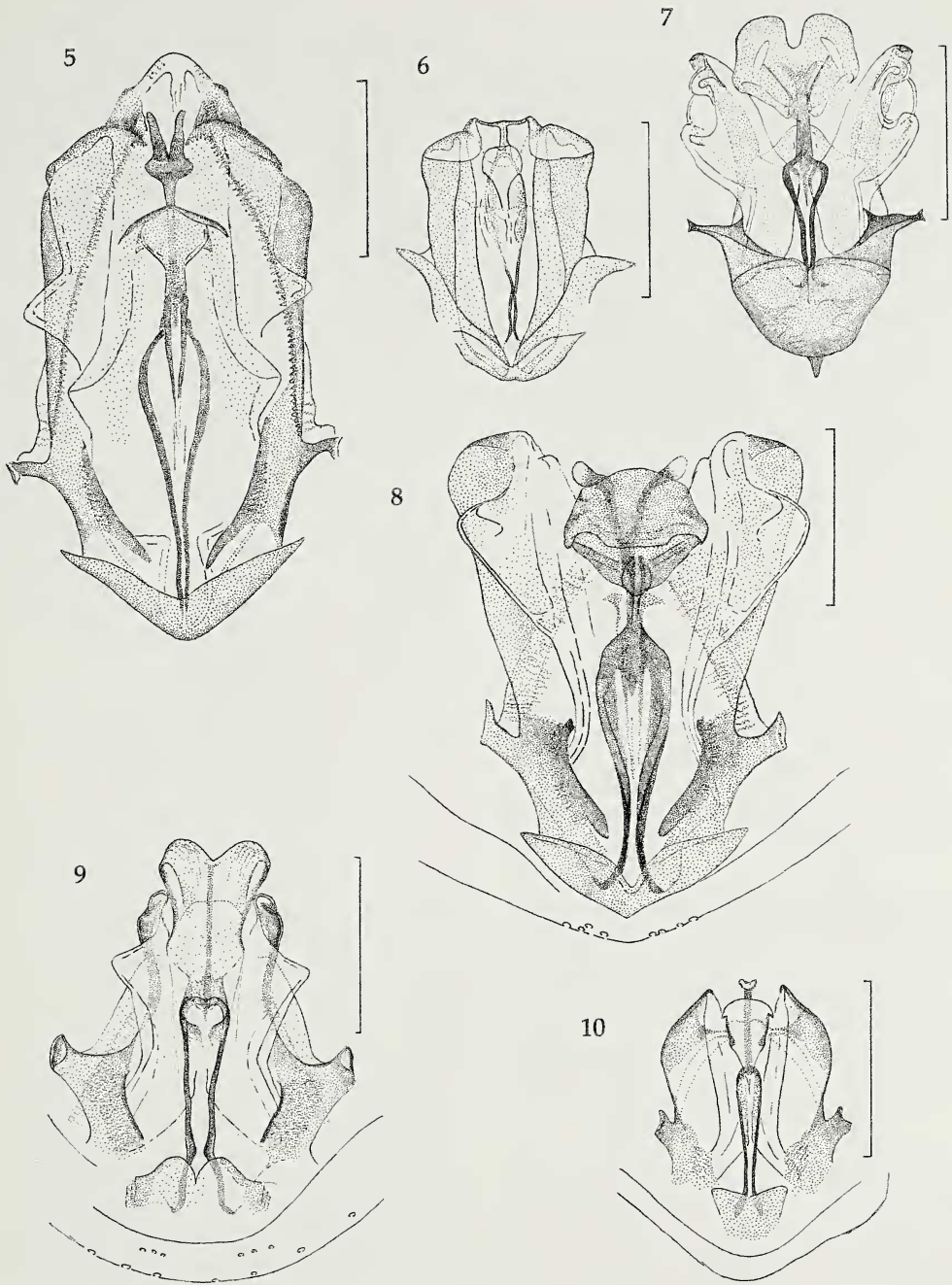


Figures 3-4.—Male genitalia, left lateral view: 3. *Diplotemnus insolitus*; 4. *Paratemnoides ellingseni*. Scale lines = 0.2 mm; abbreviations as in Figs. 1-2.

erally and enfold the proximal part of the medial diverticula on the anterior side. Here the dorsal diverticula are dominated by the lateral apodemes with their hooked branches.

Medial diverticula (Figs. 1, 2, 3 & 4: d, k).—Distally the medial diverticula extend beyond the dorsal diverticula to the level of the ejaculatory canal atrium. Here they are mostly made up of the lateral apodemes.

In many species the two medial diverticula have a prominent *extension* along the sagittal plane on the posterior side of the genital organ (Figs. 2 & 3: k). Both of these extend to the level of the ejaculatory canal atrium and are fused along the midline, forming a finger-like bulge. This is easily seen from the anterior side for instance in *Titanatemnus gigas*, *T. tessmanni*, *Cyclatemnus centralis* and *Cata-*



Figures 5–10.—Male genitalia, anterior side: 5. *Miratennus hirsutus*; 6. *Brazilatennus browni*; 7. *Tullgrenius indicus*; 8. *Diploctennus insolitus*; 9. *Atemnus politus*; 10. *Stenatennus fuchsi*. Scale lines = 0.2 mm.

temnus togoensis (Figs. 11, 14, 21, 28). In *Diploctennus insolitus* it is pointed posteriorly and can best be seen from the lateral side (Fig. 3: k). In *Oratennus loyolai* it is very conspicuous and protrudes beyond the lateral apo-

demes (Fig. 15). In others like *Paratennoides* and *Tullgrenius indicus* this extension is reduced or almost lacking (Figs. 4k, 7, 18–20, 22). Proximally, the medial diverticula are covered by the dorsals and their associated lat-

eral apodemes on the anterior side of the genital organ.

On the anteromedial side the membranous wall of both the medial diverticula is folded over, forming a longitudinal fold running from the distal end of the lateral apodeme right up to the proximal part of the same (Fig. 1d). Here the fold is covered by the lateral apodeme (Fig. 1c). In most genera the fold has a projection midway along its length. This can be distinctly pointed, as for instance in *Miratennus hirsutus*, *Atemnus politus*, *Titanatennus palmquisti* and *Cyclatennus centralis* (Figs. 5, 9, 12, 21). In *Oratennus navigator* the pointed projection typically has a small indentation (Fig. 16). *Catatennus birmanicus* and *C. granulatus* have the projection of the longitudinal fold more gently rounded, and in the latter species it has a distinct notch (Figs. 26, 27). In others, like *T. gigas*, *T. sjoestedti*, *T. tessmanni* and *Anatennus voeltzkowi* the projection is more like a lobe (Figs. 11, 13, 14, 25). *Tullgrenius indicus* is aberrant in having two lobes (Fig. 7) as is *Anatennus novaguineensis* in having three overlapping lobes (Fig. 23). In *Brazilatennus browni*, *Stenatennus fuchsi*, *Paratennoides pallidus*, *P. nidificator* and *P. salomonis* (Figs. 6, 10, 18–20) the projection of the longitudinal fold is lacking.

Ventral diverticulum (Fig. 1: h).—The anterior wall is mostly sclerotized, but can be colorless and almost transparent in some of the smaller species. Typically it is bilobed, most pronouncedly so in the *Titanatennus* species (Figs. 11, 13, 14). In the four miratennine genera this diverticulum is very wide and has a somewhat hood-like appearance (Figs. 5–8)

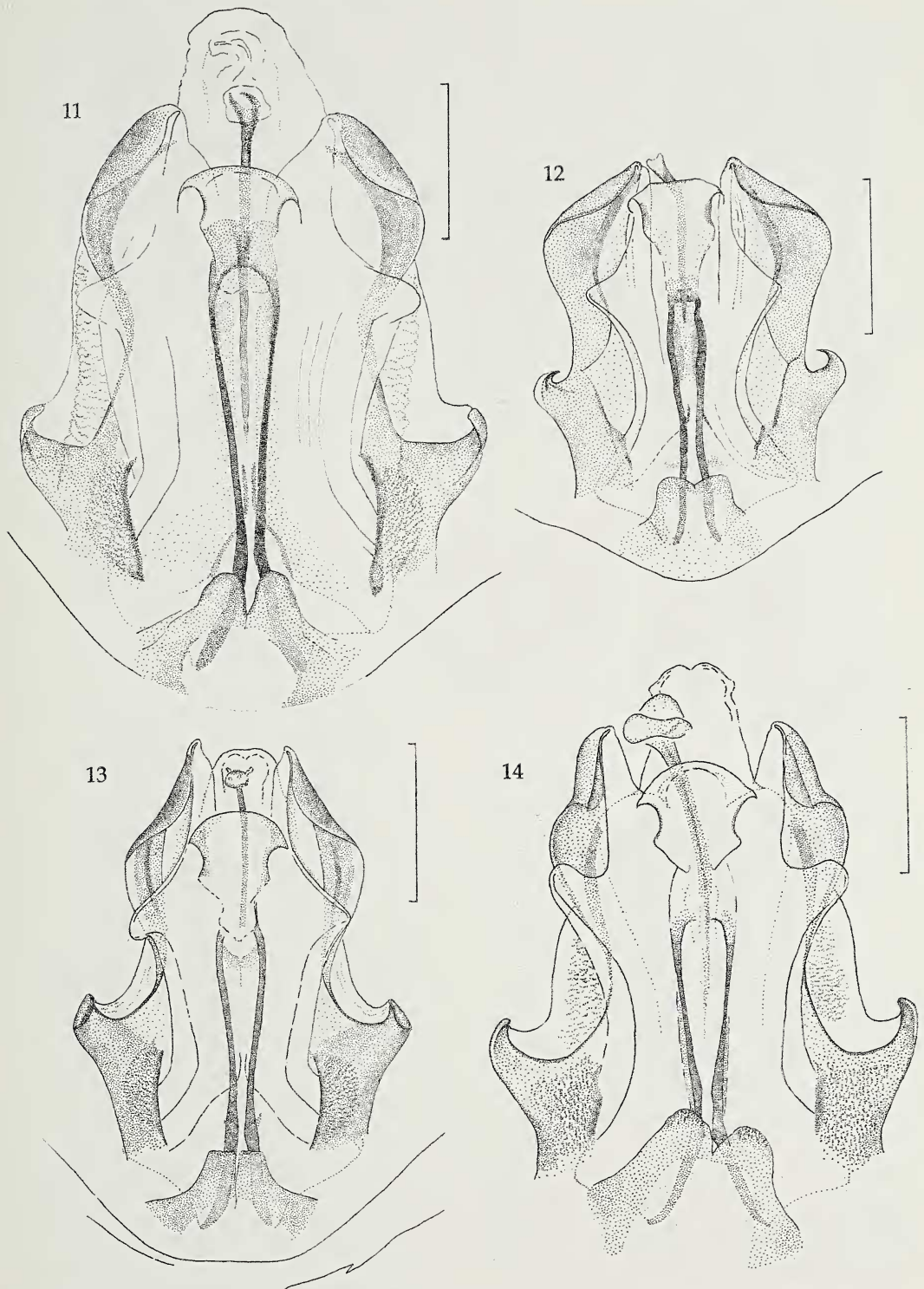
Lateral apodemes (Fig. 1: a).—The lateral apodemes are sclerotized regions formed by the anterolateral side of the two dorsal and medial diverticula. The apodemes run along either side of the lateral rods. The apodemes are oriented parallel to the rods but can be differently shaped in the different species. This is most marked at the distal end. Generally they are distinctly colored and sclerotized in the larger species, whereas in the smaller species they are delicate and almost colorless.

The lateral apodemes can be divided in 2 principal parts: A proximal part situated on the dorsal diverticula characterized by a

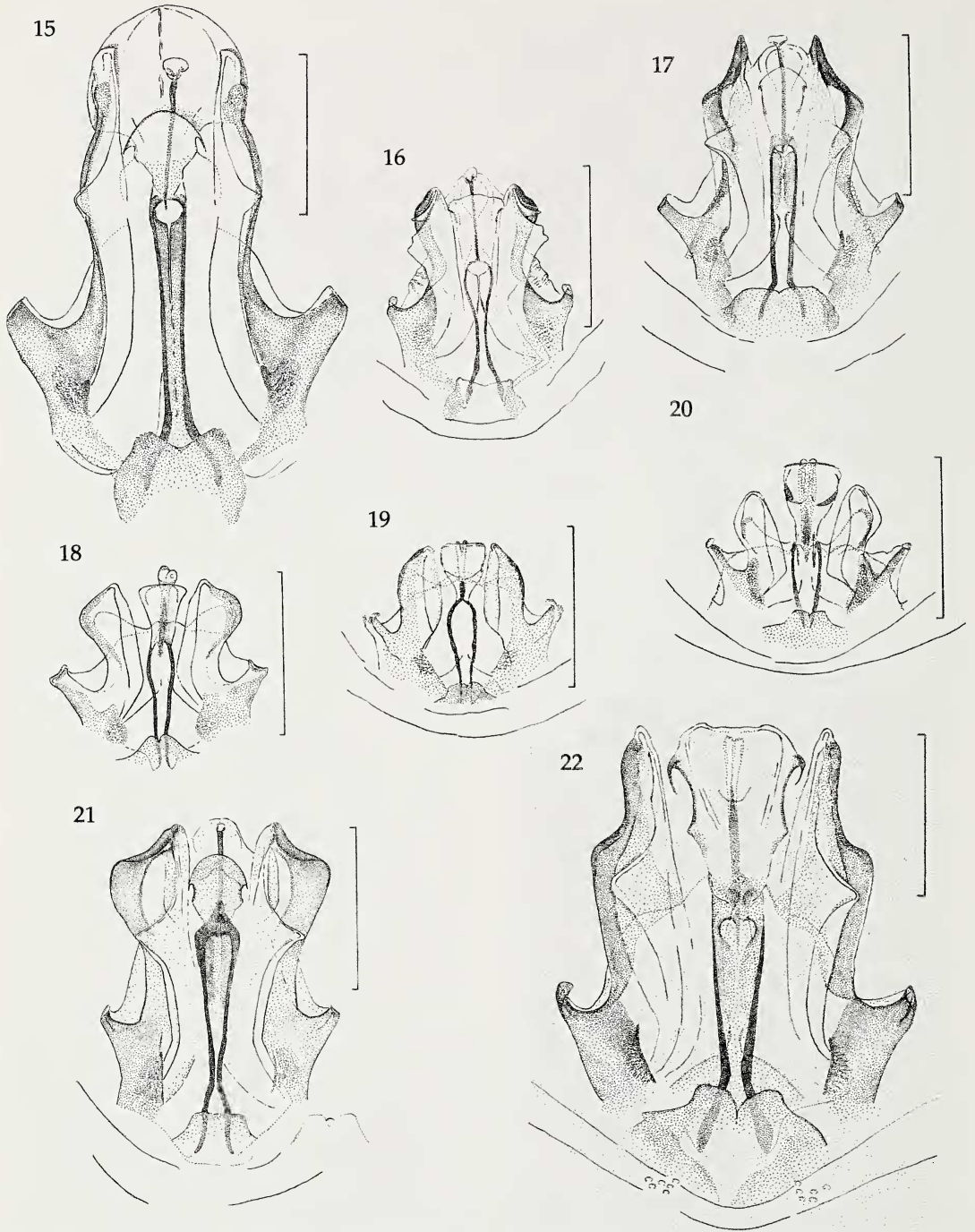
hooked branch situated on the lateral side. In the miratennines *Miratennus hirsutus*, *Brazilatennus browni* and *Tullgrenius indicus* (Figs. 5–7), the hooked branch forms an almost straight stub perpendicular to the axis of the whole organ, less so in *Diploatennus solitus* (Fig. 8). In the atennines this branch is bowed distally. In both Miratenninae and Atenninae it always terminates in a plate-like tip, perhaps with the exception of *B. browni*. This can be very pronounced as in *Atemnus politus*, *Titanatennus gigas*, *Paratennoides ellingseni* and *Anatennus voeltzkowi* (Figs. 9, 11, 22, 25). This tip is the only part of the lateral apodemes which has muscles attached to it. The proximal part always has a sclerotized rugose area on either side of the sagittal line (Fig. 1c). It is often delimited on the medial side by a darker bar. The function of this might be to reinforce the lateral apodeme when subjected to muscular contractions. In species with smaller genitalia this bar is colorless and probably reduced.

A distal part situated on the medial diverticula and more or less expanded laterally. This part of the lateral apodemes takes a wide range of different forms, being the most variable from one species to another. Though this part can be very variable it always has a lateral lip which is either bowed, rolled or wrapped up (Fig. 11). In *Titanatennus gigas* it is almost like a spoon; in *Oratennus punctatus* and *Cyclatennus centralis* it has the same shape but is bowed concavely (Figs. 11, 17 and 21). *Catatennus birmanicus*, *Anatennus voeltzkowi*, *A. angustus* and *A. orites* have a distinct inner ridge bowed into a semicircle, which make them stand apart from the others (Figs. 25, 26). In *P. ellingseni* the lateral lip is rolled into a tube (Figs. 4a, 22). In the other *Paratennoides* and in *Stenatennus fuchsi* the lateral lip is diminutive, almost lacking (Figs. 10, 18–20). In *Atemnus politus* the distal part is proportionally smaller, as is the case for *Catatennus togoensis* (Figs. 9, 28) and *Micratennus crassipes*. In the miratennines the lateral lip is transversely directed. The same is true of *Anatennus novaguineensis* and *A. javanus*, but here as if the whole genital organ has been compressed in a longitudinal direction (Fig. 23, 24).

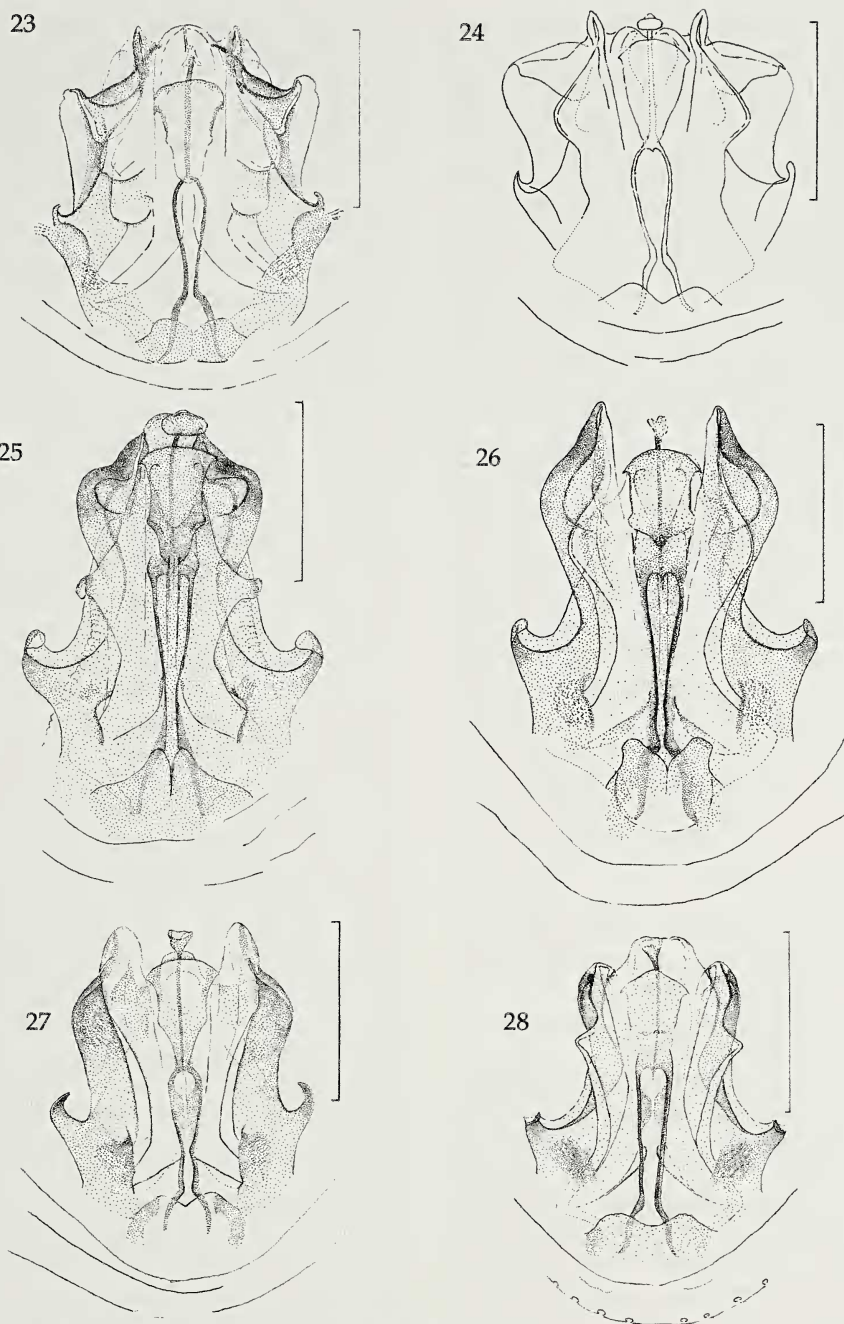
Lateral rods (Fig. 1: f).—Lateral rods, which flank the ejaculatory canal, are present in all species examined. The tips of their ends



Figures 11-14.—Male genitalia, anterior side: 11. *Titanatennus gigas*; 12. *T. palmquisti*; 13. *T. sjoestedti*; 14. *T. tessmanni*. Scale lines 0.2 mm.



Figures 15–22.—Male genitalia, anterior side: 15. *Oratemnus loyolai*; 16. *O. navigator*; 17. *O. punctatus*; 18. *Paratemnoides pallidus*; 19. *P. nidificator*; 20. *P. salomonis*; 21. *Cyclatemnus centralis*; 22. *P. ellingseni*. Scale lines = 0.2 mm.



Figures 23–28.—Male genitalia, anterior side: 23. *Anatemnus novaguineensis*; 24. *A. javanus*; 25. *A. voeltzkowi*; 26. *Catatemnus birmanicus*; 27. *C. granulatus*; 28. *C. togoensis*. Scale lines = 0.2 mm.

are always placed inside the ventral diverticulum. Here the tips diverge, except in *Mira-temnus hirsutus* and *Paratemnoides pallidus*, *P. nidificator* and *P. salomonis* (Figs. 5, 18–20). In most cases the lateral rods are bowed when seen from the anterior side, forming a

lyre-like structure before they fuse with the dorsal apodeme. Seen from the lateral side, they are mostly recurved as in *P. ellingseni* (Fig. 4f) or may be bent in a procurved angle as in *D. insolitus* (Fig. 3f).

Dorsal apodeme (Fig. 1: g).—The dorsal

apodeme is bowed in the sagittal plane, running from the lateral rods in a curve around the ejaculatory canal atrium (Figs. 3g, 4g). This structure seem to be made up of the fused elongation of the two lateral rods. In the miratemnines it is distinctly bifid at the distal end, very prominent in *Miratennus hirsutus* and *Diplotemnus insolitus* in which the dorsal apodeme is shaped like a narrow rake with two prongs (Figs. 5, 8). In the atemnines the two distal tips are almost completely joined, but can always be identified as two minute spikes or knobs lying side by side, as for instance in *T. gigas* and *P. pallidus* (Figs. 11, 18). The apodeme is distinctly colored proximally, but more or less transparent at the distal end. Muscles are connected to the distal end.

Ejaculatory canal atrium (Fig. 1: e).—The atrium of the ejaculatory canal covers the prostatic reservoir. It is bowl or cup shaped when seen laterally, fairly simply constructed in the atemnines, but more elaborate in the miratemnines (Figs. 3e, 4e). When seen from the anterior side, the atrium of the atemnines is more or less crescent-shaped on either side, marking the openings for the incoming ducts of the seminal vesicles. The distal end of the atrium is typically either procurved or flattened in the atemnines. The atrium of *Atemnus politus* is aberrant in this respect (Fig. 9). In the miratemnines the configuration of the atrium seems to differ more between the genera than is the case in the atemnines.

DISCUSSION

Characters diagnostic of the family.—The male genitalia of the Atemnidae share common features which make them stand apart from other pseudoscorpion families. Compared to the other families of the Cheliferodea, they clearly constitute a monophyletic group in this respect. The characters which unite them can be summed up in the following diagnostic description. The letters refer to those of Figs 1 and 2: (a) Distal part of lateral apodemes more or less sclerotized, especially the lateral border. The lateral border is always bowed, wrapped or rolled-up in a lateral lip, sometimes to the extent of giving the lateral apodeme a snout- or rod-like appearance; (b) Proximal part of each lateral apodeme with a hooked branch laterally. Typically these are sclerotized, but when reduced they are translucent and hard to see; (c) Prox-

imal part of each lateral apodeme furnished with a rugose darker area and delimited by a bar medially, strengthening this area; (d) Medial diverticulae more or less wrapped up on the anterior side along the sagittal line and overlying the lateral apodemes, often with a pointed or rounded projection midway; (e) Atrium of the ejaculatory canal more or less bowl-shaped; (f) Lateral rods long and conspicuous, running parallel to the sagittal line. Usually diverging proximally; (g) A long dorsal apodeme is always present, made up of the fused elongation of the lateral rods. Bifurcate or bilobate distally; (h) Anterior wall of the ventral diverticulum bilobed or bipartite; (i) Distal part of the two dorsal diverticulae are folded transversally making up the border against the medial diverticulae on the posterior side; (j) A knob-shaped apophysis present, which may have an attachment function for the posterior dorsal gland.

Affinities to other families.—The Atemnidae including the Miratemninae are placed in the Cheliferodea together with the Cheliferidae, Chernetidae and Withiidae. Harvey (1992) dealt with the affinities between these four families and placed the first three in a trichotomy because he could not find any apomorphies that might split this group in smaller entities. Proctor (1993) has pointed to the fact that the spermatophore stalk of the Cheliferidae and the Chernetidae possess a droplet that is absent in the Atemnidae and the Withiidae. This resolves the trichotomy and places the Cheliferidae and Chernetidae in a clade separated from the other two. Although this does not imply any closer connection between the atemnids and the withiids, it might be noted that the overall configuration of the male genitalia of atemnids seem to be closer to the withiids than to the other two families.

In Chernetidae the almost circular apodemes have the distal ends fused or united, this configuration seem to be very consistent and very different from that of the atemnids. The absence of lateral rods in the chernetids also make them stand apart from the atemnids.

When considering the Cheliferidae there are some similarities. They have the same long, parallel lateral rods as the Atemnidae but there is one significant difference, at least when compared to *Chelifer cancroides* and *Dactylochelifer latreillii* as pictured by Vachon (1938a) and Legg and Jones (1988). This is

that the proximal ends of the lateral rods are merged in the cheliferids, which is never the case in the atemnids investigated by me. Another very important difference between the two families is the presence of ram's horn organs in the cheliferids, which are absent in the atemnids.

This leaves us with the Withiidae, which has the long, parallel lateral rods not merged proximally, just as in the Atemnidae. Moreover, the lateral apodemes of the withiids have the same pronounced hooked branches as in the atemnids, as shown by Heurtault (1971) and Harvey (1988). Judged from these character states of the male genitalia, I consider the Withiidae as the sister group to the Atemnidae.

Differences between Atemninae and Miratemninae.—Despite the differences between the genera and between the species, the overall structures of the male genitalia and their orientation are remarkably uniform in atemnines and miratemnines. However, because the miratemnines have earlier been raised to family level partly because of certain characteristics of their male genitalia, it seems appropriate to discuss their affinities here.

When Vachon (1938a) compared the male genitalia of *Titanatemnus congicus*, *Atemnus politus* and *Catatemnus schlottkei* with those of *Miratemnus hispidus*, he concluded that the apodemes of the latter differed in being directed in the opposite direction to those of the former. He also concluded that in this respect *Miratemnus* came closer to *Withius* than to the other three. Dumitresco & Orghidan (1969, 1970) used this as an important argument in favor of raising the miratemnines to family level.

However Vachon's observations on atemnines and miratemnines are not based on fundamental differences in the structure of the genitalia or in the mutual arrangement of these structures, a fact that Vachon certainly must have been aware of. The differences simply depend on the orientation of the genitalia. When examined in situ, the genitalia of the atemnines *Titanatemnus* and *Atemnus* are bent anteriorly from the genital opening, whereas those of *Miratemnus* are bent posteriorly. In a ventral view, then, in the atemnines one actually observes the organ with the anterior side lying nearest to the sternites, while in the miratemnines *Miratemnus* and *Diplo-*

temnus one has the posterior side nearest to the sternites, as shown by the side view of *Paratemnoides ellingseni* and *Diplo-*
temnus insolitus (Figs. 3, 4).

Hence, the crucial point is whether this difference in bending is sufficient to justify a separation into two families. In fact, this difference is not absolute between the two groups. The miratemnine *Tullgrenius* has an organ in which the distal part is bent at a 45° angle anterior to the genital aperture and in the Asiatic and American atemnids of the genus *Paratemnoides* the whole organ is directed almost dorsoventrally. Harvey (1988) observed that the orientation of the lateral rod in *Paratemnoides assimilis* was more similar to Miratemninae than to the atemnines *Atemnus* and *Titanatemnus*. Obviously the angle of the genitalia varies in both atemnines and miratemnines and does not provide a useful diagnostic difference between the groups.

Even if there are no fundamental differences separating the miratemnines and atemnines, the morphology of the male genitalia of miratemnines shows characteristics which separate them from the atemnines. These might be used as diagnostic character states of the miratemnines. They can be summarized as follows: (a) The anterior wall of the ventral diverticulum is very wide, covering the most proximal part of the lateral apodemes and having a hood-like appearance. (b) The hooked branch of the lateral apodemes is straight when seen from the anterior side, mostly perpendicular to the longitudinal axis of the whole organ. (c) The distal end of the dorsal apodeme is distinctly bifurcated into two separate branches, which are not merged as in the atemnines.

Differences between genera.—The investigation of the genitalia of the different species reveals a very striking result. The variation between the different species within a genus is often greater than the variations between species from different genera. The obvious explanation must be that several of the genera are not monophyletic. The reason for this might be that the delimitation of the genera is based on external morphological characters which in some cases are difficult to observe and of dubious diagnostic value. This relates to both discrete and continuous characters. For instance, size is used by Beier (1932a, 1932b) as a diagnostic character to separate *Titana-*

temnus from *Cyclatenuus* and *Paratenuoides* and *Oratenuus* is separated from *Atemnus*, *Anatenuus* and *Micratenuus* by the slimmer stalk of the patella.

Another important diagnostic character is the presence or absence of a transverse groove or furrow on the carapace. This is used as a major distinguishing feature to separate several genera of Atemninae. According to Beier (1932a, 1932b) those atemnines with a groove are *Catatenus*, *Metatenus*, *Stenatenus* and *Tatenus*. This follows the original description by Thorell (1889) of *Chelifer birmanicus* (the type species of *Catatenus*) where he states that the carapace has a "sulco transverso singulo", i.e. a single transverse groove or furrow. This groove can be very difficult to define, and any slight depression on the carapace might have been interpreted as a groove. This problem is discussed by With (1906) who makes a distinction between groove, stripe and line; in *C. birmanicus* he described this character as a transverse stripe and in *C. concavus* and *C. monitor* as a transverse line, all three later included in the genus *Catatenus* by Beier (1932a, 1932b). In fact, when scrutinized, the transverse stripe of *C. birmanicus* actually is the borderline between the dark colored frontal part and the pale posterior part of the carapace, at least in those syntypes which have been available to me deposited in Naturhistoriska Riksmuséet in Stockholm and in Zoological Museum in Copenhagen. The absence of a furrow or groove is particularly obvious when the specimens are looked at from the lateral side, seeing the outline of the carapace.

However, in several other species where the specimens are prepared, a sort of transverse fold can be observed in the same area, as if a narrow part of the anterior of the carapace is wrapped over the posterior. Specimens of *Catatenus togoensis*, *C. granulatus*, *Tatenus femoratus* and *Stenatenus fuchsi* show this fold. Another species, *Micratenuus crassipes*, does have a transversal fold, although the genus was originally described as being without a groove on the carapace. The same fold is pronounced in *Miratenuus* and *Diploatenus* but very weak or absent in *Tullgrenius*, although the groove as such is evident in all Miratenuinae. On the other hand, the syntype of *Catatenus birmanicus*, the type species of that genus, definitely does not have a fold. To

sum up, this character is obviously not a discrete one, but varies through different phases from a very distinct groove accompanied with a fold, to a groove or slight depression with no fold or to a fold with no groove; or just a difference in color and sclerotisation between the anterior and posterior part. This diversity might be looked at as the different expressions of the vestigial border between the head and the first segment of the carapace.

Variation within genera.—*Anatenuus species* (Figs. 23–25): Of the three species figured here, *A. javanus* (the type species) and *A. novaguineensis* seem to constitute a group with synapomorphic character states. Their peculiar shape, as if the whole organ has been compressed in a longitudinal direction, distinguishes them from all other species compared here. This compression has placed the lateral lip in an almost transversal position, ending in a small projecting snout at the distalmost end. Another shared characteristic which makes them stand apart from other species is their comparatively small hooked branches. *Anatenuus subvermiformis* has the same transversally placed lateral lips but lacks the projecting snout and has the same small hooked branches. There can be no doubt that these three species are closely related. *Anatenuus elongatus* has the same transversally directed lateral lips and the same projecting snout at the distalmost end as in *A. javanus* and *A. novaguineensis*, but it has the hooked branches projecting wider to each side.

In contrast, *A. voeltzkowi* has the lateral apodemes quite differently shaped. The lateral lips of this species have a strongly curved medial border, shared with *Catatenus birmanicus* and *A. angustus*. The shape of the ejaculatory canal atria is also very similar. Although the shape of the ventral diverticulum and the projection of the longitudinal folds are different and more reminiscent of those of *Titanatenus*, the overall similarity indicates a closer connection between these two species than existing systematic positions implies.

Anatenuus angustus is identical to *C. birmanicus* in genital configuration as well as in external morphology, apart from carapace, as noted in the species list. The male genitalia of *A. orites* are very similar to *A. angustus*. The only difference is that the whole organ of *A. orites* is slightly slimmer across the lateral lips

of the lateral apodemes and their lateral incurvation are less pronounced than in *A. angustus*. Taking all this into account the genus *Anatemnus* seems to be polyphyletic. At least, based on the male genitalia, it can be roughly divided into two groups, one very close to *C. birmanicus* and another standing apart from all other species investigated.

Catatemnus species (Figs. 26–28): This is another genus in which there are few common features in the character states of the genitalia. The ventral diverticulum of *Catatemnus granulatus* and *C. togoensis* are similar but differ from the more deeply bilobed ventral diverticulum of *C. birmanicus* (the type species). The longitudinal folds of the medial diverticula are different in all three species, as are the lateral lips of the lateral apodemes and the ejaculatory canal atria do not have any striking resemblances. However, when external morphology is considered, both *C. granulatus* and *C. togoensis* have a transverse fold on the carapace, which is lacking in *C. birmanicus*. The trochanter of the pedipalps has a rounded dorsal bulge in the former two, whereas in *C. birmanicus* this bulge is pointed. Seen in lateral view, the patella is bulb- or vase-shaped in *C. birmanicus*, but in *C. granulatus* and *C. togoensis* it is more elongated and spindle shaped. On the other hand the presence of discal seta on the tergites of all three species might indicate relationship.

In this context it is worth noticing that *Tatemenus femoratus* has the transverse fold on the carapace, present in *C. granulatus* and *C. togoensis* but lacking in *C. birmanicus*. The genitalia have the characteristic configuration of the lateral lip seen in *C. birmanicus* and *Anatemnus voeltzkowi*, even if the lateral border is almost straight rather than incurved, more like that in *A. orites*. The ventral diverticulum of *T. femoratus* is distinctly bilobed, much as in *A. voeltzkowi*, but the longitudinal fold is almost straight with a small fin-like projection midway, not gently curved as in *C. birmanicus* and *A. voeltzkowi*. Another species worth mentioning in connection with *Catatemnus* is *Micratemnus crassipes*. This species have genitalia with a strong resemblance to *C. togoensis*, especially the distal part of the lateral apodeme, even if the whole organ is smaller and corresponding to the smaller size of the animal.

Cyclatemnus species (Fig. 21): The species

C. burgeoni, *C. dolosus*, *C. globosus*, *C. granulatus* and *C. robustus* have genitalia almost identical to those of *Cyclatemnus centralis* (the type species), as does *C. minor* although these are smaller. The differences between them are confined to slight variations in the curvature of the lateral lips of the lateral apodeme. At least when considering the male genitalia, this genus seem to be very homogeneous. However, *C. granulatus* is divergent in its external morphology. It has discal seta on tergites IV–X, as in *Catatemnus*, this is in accordance with the observation of Vachon (1952). The other species lack the discal seta on the tergites IV–VIII, which contradicts the observations of Mahnert (1983) on *Cyclatemnus centralis*.

Athleticatemnus pugil (the type and sole species) bears a strong likeness to *C. granulatus* in external morphology as noted earlier. The genitalia of *A. pugil* resemble those of *Cyclatemnus*, but the curvature of the distal part of the lateral apodeme is more straight angled, the lateral lip is slimmer and the most distal part of the lip is drawn up in a dorsoventral direction.

Oratemnus species (Figs. 15–17): It is hard to find any common denominators in the genitalia of the three species treated here that might be called apomorphic character states and thus make them stand apart from the others as a single entity. They all have a rather shallow bilobation of the ventral diverticulum but then so have several others, such as *Stenatemnus fuchsi*, *Catatemnus granulatus* and *C. togoensis*. The ejaculatory canal atrium of *O. loyolai* is reminiscent of that of *Cyclatemnus centralis*, whereas that of *O. punctatus* is more like the atrium of *Anatemnus javanus* or *Stenatemnus fuchsi*. The atrium of *O. navigator* is intermediate between that of *Anatemnus novaguineensis* and *Catatemnus togoensis*. The most divergent character among the three is the configuration of the lateral lips. *Oratemnus punctatus* has the lateral lip formed almost like those of *Cyclatemnus* or *Titanatemnus*, in fact, the organ as a whole might easily be that of a *Cyclatemnus* species. The lateral lips of *O. loyolai* do show some resemblance to those of *Paratemnoides ellingseni*, but *O. loyolai* differs clearly in the bulging shape of the medial diverticular extension. *Oratemnus navigator* stands apart from the other two in having a very small lateral lip

and by having an additional fin in front of the projection of the longitudinal fold. In its external morphology *O. navigator* differs mostly in having discal seta on the tergites, which are absent in the other two. Judged from the configuration of the male genitalia in the three species I have investigated, the genus *Oratemnus* seems to be polyphyletic.

Paratemnoides species (Figs. 4, 18–20, 22): In this genus the three species *P. nidificator*, *P. pallidus* (the type species) and *P. salomonis* are very much alike; they are only separated by minor differences in the proportions of the hooked branch and the distal part of the lateral apodeme. Although the differences are small they seem to be very constant in the specimens investigated by me, indicating that they are specific. The aberrant species is obviously *P. ellingseni*, which clearly stands apart from the others in the configuration of the genitalia. Except for the size alone, the shape of the lateral apodemes are totally different, the longitudinal fold has a pronounced projection, the lateral rods are diverging proximally inside the ventral diverticulum, and the ejaculatory canal atrium has crescent shaped openings on either side which are lacking in the other *Paratemnoides*. Considering these characters, it is hard to believe that *P. ellingseni* could be congeneric with the others. The external morphology is indeed very similar, which of course is the main reason that this species has been placed in *Paratemnoides*. However there are some differences: the trochanter of *P. ellingseni* has a pointed bulge dorsally, whereas in the others this bulge is less pronounced and rounded; the shape of the patella in lateral view is almost flattened in *P. ellingseni*, like a short sausage, whereas in the others it is bean-shaped. The last species on my list, *Paratemnoides insubidus*, is very close to *P. ellingseni*. Its genitalia are almost identical, but it differs in the external morphology by having a patella that is wider seen in lateral view, having a shape like the seed bulb of a poppy. The trochanter, however, has the same pointed bulge dorsally as *P. ellingseni*. Considering the differences in this group, I must conclude that this genus is polyphyletic with *P. ellingseni* and *P. insubidus* forming a separate group that stands apart from the others.

Titanatemnus species (Figs. 11–14): The species examined in this genus seem to con-

stitute a fairly homogenous group, perhaps with *T. palmquisti* being the most divergent. All other species have a pronounced bipartite ventral diverticulum, a lobed or rounded projection on the longitudinal fold, a significant extension of the medial diverticulae and a characteristic form of the ejaculatory canal atrium. *Titanatemnus natalensis* is very close to *T. gigas* (the type species) in genital configuration, with the extension of the medial diverticulae being less protruding and the lateral lip of the lateral apodeme slightly straighter, more like in *T. sjoestedti*. However *T. palmquisti* is aberrant in having a less cleft bilobation of the ventral diverticulum, a more pointed projection on the longitudinal folds and slightly more transversely directed lateral lips. The overall configuration lies somewhere between the *Titanatemnus* and *Cyclatemnus* type. In the light of this it is interesting to note that Mahnert (1983) has pointed to some affinities between this species and *Cyclatemnus fallax* and *C. burgeoni*.

In conclusion, when considering the configuration of the male genitalia within existing genera, it is obvious that the diagnostic characters currently used have led to misplacements and to systematic groupings that do not reflect true phylogenetic relationship inside the family. Admittedly, the external morphology has only occasionally been taken into consideration in the present discussion and has not been treated in a systematic manner. A more meticulous treatment of these characters in a cladistic analysis, together with those of genitalia, should provide a clearer understanding of relationships between the genera.

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LITERATURE CITED

- Balzan, L. 1888. Chernetidae nonnullae Sud-Americanae. Asuncion, Paraguay. III.
- Balzan, L. 1890. Revisione dei Pseudoscorpioni del Bacino dei Fiumi Paraná e Paraguay nell'America Meridionale. *Annali del Museo Civico di Storia Naturale di Genova* (2a) 9:401–454.
- Balzan, L. 1892. Voyage de M. E. Simon au Venezuela (Décembre 1887–Avril 1888). *Arachnides. Chernetes (Pseudoscorpiones). Annales de la Société Entomologique de France* 60:497–552.
- Beier, M. 1932a. Revision der Atemnidae (Pseudoscorpionidea). *Zoologische Jahrbücher, Abteilung für Systematik, Ökologie und Geographie der Tiere* 62:547–610.
- Beier, M. 1932b. Pseudoscorpionidea II. Subord. C. Cheliferinea. *Tierreich* 58:i–xxi, 1–294.
- Beier, M. 1972. Pseudoscorpionidea aus dem Parc national Garamba. *Exploration Parc National de la Garamba, Mission H. de Saeger* 56:2–19.
- Beier, M. 1979. Neue afrikanische Pseudoscorpione aus dem Musée Royal de l'Afrique Centrale in Tervuren. *Revue de Zoologie Africaine* 93(1): 101–113.
- Chamberlin, J.C. 1931. The arachnid order Chelonethida. *Stanford University Publications, Biological Sciences* 7(1):1–284.
- Chamberlin, J.C. 1939. New and little-known false scorpions from the Marquesas Islands. *Bulletin of the Bernice P. Bishop Museum* 142:207–215.
- Chamberlin, J.C. 1947. Three new species of false scorpions from the islands of Guam. *Occasional Papers of the Bernice P. Bishop Museum* 18(20): 305–316.
- Dashdamirov, S. & W. Schawaller. 1993. Pseudoscorpions from Middle Asia, Part 3 (Arachnida: Pseudoscorpiones). *Stuttgarter Beiträge zur Naturkunde, Ser. A (Biologie)* 497:1–16.
- Dumitresco, M. & T. Orghidan. 1969. Sur deux espèces nouvelles de Pseudoscorpions (Arachnides) lithoclasicoles de Roumanie: *Diplothemnus vachoni* (Atemnidae) et *Dactylochelififer marlausicolus*. *Bulletin du Muséum National d'Histoire Naturelle, Paris* (2) 41:675–687.
- Dumitresco, M. & T. Orghidan. 1970. Cycle du développement de *Diplothemnus vachoni* Dumitresco et Orghidan, 1969, appartenant à la nouvelle famille des Miratemnidae (Arachnides, Pseudoscorpions). *Bulletin du Muséum National d'Histoire Naturelle, Paris* (2) 41(supplément 1): 128–134.
- Ellingsen, E. 1906. Report on the pseudoscorpions of the Guinea Coast (Africa) collected by Leonardo Fea. *Annali del Museo Civico di Storia Naturale di Genova* (3) 2:243–265.
- Ellingsen, E. 1908. Pseudoscorpiones. In Strand, E., *Arachniden aus Madagaskar. Zoologische Jahrbücher, Systematik (Ökologie), Geographie und Biologie* 26:487–488.
- Harvey, M.S. 1988. Pseudoscorpions from the Krakatau Islands and adjacent regions, Indonesia (Chelicerata: Pseudoscorpionida). *Memoirs of the Museum of Victoria* 49:309–353.
- Harvey, M.S. 1991. *Catalogue of the Pseudoscorpionida*. Manchester University Press, Manchester.
- Harvey, M.S. 1992. The phylogeny and classification of the Pseudoscorpionida (Chelicerata: Arachnida). *Invertebrate Taxonomy* 6:1373–1435.
- Heurtault, J. 1970. Pseudoscorpions du Tibesti (Tchad). III. Miratemnidae et Chernetidae. *Bulletin du Muséum National d'Histoire Naturelle, Paris* (2) 42:192–200.
- Heurtault, J. 1971. Chambre génitale, armature génitale et caractères sexuels secondaires chez quelques espèces de Pseudoscorpions (Arachnides) du genre *Withius*. *Bulletin du Muséum National d'Histoire Naturelle, Paris* (2) 42:1037–1053.
- Legg, G. 1974. A generalised account of the male genitalia and associated glands of pseudoscorpions (Arachnida). *Bulletin of the British Arachnological Society* 3:66–74.
- Legg, G. & R.E. Jones. 1988. Pseudoscorpions (Arthropoda; Arachnida). *Synopsis of the British Fauna (New Series)* 40:1–159. The Linnean Society of London.
- Mahnert, V. 1983. Die Pseudoscorpione (Arachnida) Kenyas VII. Miratemnidae und Atemnidae. *Revue Suisse de Zoologie* 90:357–398.
- Proctor, H.C. 1993. Mating biology resolves trichotomy for cheliferoid pseudoscorpions (Pseudoscorpionida, Cheliferoidea). *Journal of Arachnology* 21:156–158.
- Schawaller, W. 1994. Pseudoscorpione aus Thailand (Arachnida: Pseudoscorpiones). *Revue Suisse de Zoologie* 101(3):725–759.
- Thorell, T. 1889. XXI. Aracnidi Artrogastri Birmani raccolti da L. Fea nel 1885–1887. Ordo Chelonethi (In: *Viaggio di Leonardo Fea in Birmani e Regione Vicine*). *Annali del Museo Civico di Storia Naturale di Genova* (2) 7:591–607.
- Tullgren, A. 1907. Zur Kenntnis aussereuropäischen Chelonethiden des Naturhistorischen Museums in Hamburg. *Mitteilungen aus dem Naturhistorischen Museum in Hamburg* 24:21–75.
- Vachon, M. 1938a. Recherches anatomiques et biologiques sur la reproduction et le développement des Pseudoscorpions. *Annales des Sciences Naturelles, Zoologie* (11) 1:1–207.
- Vachon, M. 1938b. Voyage en A. O. F. de L. Berland et J. Millot. IV. Pseudoscorpions. Première note. Atemnidae. *Bulletin de la Société Zoologique de France* 63:304–315.
- Vachon, M. 1952. La réserve naturelle intégrale du

- Mt. Nimba. II. Pseudoscorpions. Mémoires de l'Institut Français d'Afrique Noire 19:17–43.
- Weygoldt, P. 1970. Vergleichende Untersuchungen zur Fortpflanzungsbiologie der Pseudoscorpione II. Zeitschrift für Zoologische Systematik und Evolutionforschung 8:241–259.
- With, C.J. 1906. The Danish Expedition to Siam 1899–1900. III. Chelonethi. An account of the Indian false-scorpions together with studies on the anatomy and classification of the order. Det Kongelige Danske Videnskabs Selskabs Skrifter 7(III):1–214.
- With, C.J. 1908. An account of the South-American Cheliferinae in the collections of the British and the Copenhagen Museums. Transactions of the Zoological Society of London 18:217–340.
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